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MEETING REVIEW

Auxin 2016: a burst of auxin in the warm south of China

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ABSTRACT

The luxurious vegetation at Sanya, the most southern location in China on the island of Hainan, provided a perfect environment for the 'Auxin 2016' meeting in October. As we review here, participants from all around the world discussed the latest advances in auxin transport, metabolism and signaling pathways, highlighting how auxin acts during plant development and in response to the environment in combination with other hormones. The meeting also provided a rich perspective on the evolution of the role of auxin, from algae to higher plants.

KEY WORDS: Conference, Auxin, Plant biology

Introduction

By necessity, land plants have acquired signaling and metabolic mechanisms that allow them to adapt successfully to their environment. Plant hormones are of particular importance, mediating developmental changes by integrating and coordinating environmental and endogenous signals. Auxin – a key plant hormone – plays a prominent role in regulating plant developmental processes, and delineating its role is therefore the subject of intensive investigation. As we discuss below, new insights into these processes were presented at the Auxin 2016 meeting, which was held in Sanya, China, and was organized by Jennifer Nemhauser (University of Washington, Seattle, WA, USA), Dolf Weijers (University of Wageningen, The Netherlands) and Zhenbiao Yang (University of California, Riverside, CA, USA), with the local support of Choazu He (Hainan University, China).

Controlling auxin levels: metabolism and transport

Local changes in metabolic activities have recently emerged as key determinants that control the distribution of auxin (indole-3-acetic acid or IAA) during plant development. The major auxin biosynthesis pathway is currently thought to be a two-step pathway (Fig. 1) that modifies L-tryptophan (L-Trp) and involves TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1/TRYPTOPHAN AMINOTRANSFERASE-RELATED (TAA1/TAR) and YUCCA enzymes (Ljung, 2013). Although several alternative pathways have been identified, their contribution to auxin biosynthesis remains unclear, notably because the enzymes implicated in these pathways are often encoded by multigene families. Yunde Zhao (University of California, San Diego, CA, USA) showed how they are using an innovative CRISPR-Cas9 approach (Gao et al., 2016) to rapidly obtain multiple mutants and test the contribution of these pathways to development. Auxin homeostasis is also regulated by the conversion of indole-3-butyric acid (IBA) to IAA (Strader et al., 2011). Lucia Strader (Washington University, Saint Louis, MO, USA) presented the identification and functional characterization of an *Arabidopsis* transporter of IBA1 (TOB1), which might sequester IBA in vacuoles to limit its contribution to the intracellular auxin pool. Karin Ljung (Swedish University of Agricultural Sciences, Umeå, Sweden) further discussed how the oxidation of auxin to 2-oxindole 3-acetic acid (oxIAA), which is catalyzed by DIOXYGENASE FOR AUXIN OXIDATION1 (DAO1), leads to irreversible inactivation and degradation of auxin. Accordingly, an *Arabidopsis dao1* mutant shows subtle but auxin-related phenotypes, notably in root hairs (Porco et al., 2016). To better monitor auxin levels *in vivo*, Ole Herud from Gerd Jürgens' laboratory (Max Planck Institute for Developmental Biology, Tübingen, Germany) reported an attempt to modify an *Escherichia coli* Trp sensor (Marmorstein et al., 1987) to create a novel auxin sensor based on Förster Resonance Energy Transfer (FRET). The insights this new biosensor could provide are undoubtedly eagerly awaited.

The spatiotemporal distribution of auxin during development is also mediated by the coordinated activity of several carriers, including AUXIN1/LIKE-AUX1 (AUX1/LAX) auxin influx facilitators and PIN protein efflux facilitators (Sauer et al., 2013), and the directionality of polar auxin transport is critically determined by the asymmetrical localization of PIN proteins (Wisniewska et al., 2006). Claus Schwechheimer (Technical University of Munich, Germany) discussed the role of the *Arabidopsis* serine/threonine kinase D6 PROTEIN KINASE (D6PK) in regulating auxin transport. His group had previously shown that D6PK directly phosphorylates and activates PIN transporters without affecting their polar distribution (Zourelidou et al., 2014). Using PIN1 phosphosite-specific antibodies, they now reported that phosphorylated PIN1 can be found at both basal and apical plasma membranes, raising questions about the current model of phosphorylation-dependent control of PIN1 polarity.

The chemical Endosidin 16 (ES16) was presented by Ruixi Li (Southern University of Science and Technology, Shenzhen, China) as a new tool for analyzing auxin transport. ES16 was originally isolated as a pollen germination inhibitor targeting vesicular trafficking, and Li's work now shows that ES16 interferes with PIN apical polarity through the Rab-GTPase A2a trafficking pathway (Li et al. 2016). In addition, Juan Dong (Waksman Institute of Microbiology, Rutgers University, Piscataway, NJ, USA) showed that INTERACTOR OF CONSTITUTIVELY ACTIVE ROP 1 (ICR1), which is involved in establishing auxin maxima (Hazak et al., 2014), plays a role in stomata cell polarization, providing negative regulation of BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE (BASL). This raises interesting questions about the potential universality of the mechanisms used for controlling BASL and PIN protein polarity.

Tuning the dynamics of auxin signaling

A major breakthrough in our understanding of auxin signaling was the identification of TIR1/AFB1-5 F-box proteins as co-receptors

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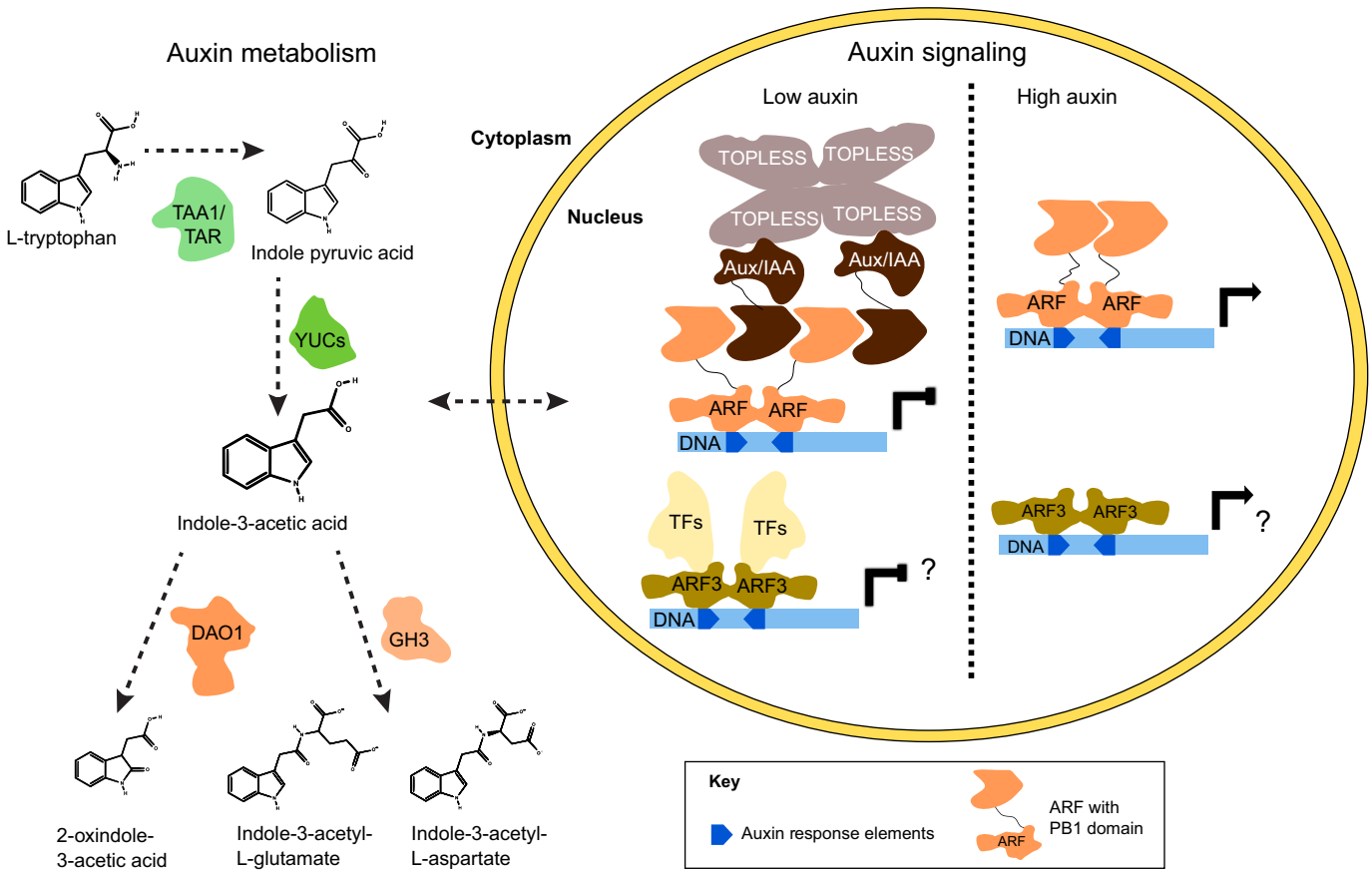

Fig. 1. Key aspects of auxin metabolism and signaling. The spatial control of auxin biosynthesis and signaling is essential for the action of this key hormone during plant development. Some of these control mechanisms were discussed in the meeting and are summarized in this figure. The main biosynthetic pathway for auxin (indole-3-acetic acid, IAA) is shown. It involves the enzymes TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1/TRYPTOPHAN AMINOTRANSFERASE-RELATED (TAA1/TAR) and YUCCA (YUC). Auxin levels are also regulated by oxidation and conjugation, both of which involve a number of enzymes; only the two enzymes discussed in the main text [DIOXYGENASE FOR AUXIN OXIDATION1 (DAO1) and GH3] are depicted here. Auxin then regulates transcription in the nucleus by triggering the degradation of Aux/IAAs, thereby releasing auxin response factors (ARFs) from their repression. Repression by auxin/IAAs is due in large part to their capacity to recruit the TOPLESS co-repressor. Different types of complexes that potentially bind to promoters of target genes are represented on the figure. Auxin can also directly regulate the interaction between ARF3 and other transcription factors (TFs), as depicted. See main text for more details.

for auxin (Chapman and Estelle, 2009). These proteins are incorporated into SKP1-CULLIN-F-BOX (SCF) complexes, with auxin allowing TIR1 and AFBs to interact with Aux/IAA transcriptional repressors. This triggers the ubiquitylation and degradation of Aux/IAAs, thereby relieving auxin response factors (ARFs) from Aux/IAA regulation (Fig. 1). It was previously shown that *tir1afb1afb2afb3* quadruple mutants are viable (Dharmasiri et al., 2005), but Mark Estelle (University of California, San Diego, Ca, USA) now reported that the sextuple mutant for TIR1/AFBs is embryo lethal. This strongly supports the idea that TIR1/AFBs define the primary pathway for auxin-regulated transcription. Although the conserved domain II of Aux/IAAs – the auxin-binding domain of Aux/IAAs – is essential for Aux/IAA ubiquitylation, the sequences flanking the domain II have been shown to influence Aux/IAA degradation rates (Moss et al., 2015). Luz-Irina Calderon Villalobos (Leibniz Institute of Plant Biochemistry, Germany) presented further evidence demonstrating that the domain II-flanking sequences are key for Aux/IAA biochemical properties, as differences in ubiquitylation and degradation rates of a sister pair of Aux/IAAs appear to result only from changes in these sequences.

Several presentations highlighted how the auxin signaling is subjected to feedback. For example, Hongwei Xue (Shanghai Institute for Biological Sciences, CAS, Shanghai, China) reported the identification of PROTEASOME REGULATOR1 (PTRE1), which positively regulates 26S proteasome activity (Yang et al., 2016). Xue showed that auxin can inhibit 26S proteasome activity, possibly by changing PTRE1 subcellular localization, highlighting that auxin signaling feeds back on proteasome activity. Neha Bhatia from Markus Heisler's laboratory (EMBL, Heidelberg, Germany) showed that the expression of MONOPTEROS(MP)/ARF5 correlates with auxin distribution in the shoot apical meristem (Bhatia et al., 2016). This positive feedback of auxin on MP was already known (Lau et al., 2011), but this identifies a major role for this feedback in allowing auxin to shape its own signaling domains in a tissue during development. A significant number of Aux/IAAs are regulated by ARFs, but little is known about other regulatory circuits that can control Aux/IAA expression. Eilon Shani (Tel Aviv University, Tel Aviv, Israel) described work, which was conducted in Tel Aviv and in Mark Estelle's laboratory, using yeast one-hybrid (Y1H) to identify over 400 putative upstream regulators of Aux/IAA, suggesting that Aux/IAAs might be seen as hubs that fine-tune auxin responses. Stéphanie Robert (Swedish University of Agricultural Sciences, Umeå, Sweden) used a chemical genomic screen to identify four new chemicals that likely interfere with the interaction between TIR1/AFBs and specific subsets of Aux/

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IAAs. Treatment with these chemicals could be used to further understand how various Aux/IAAs contribute to regulating plant development. Fine-tuning of auxin responses also occurs directly through ARF regulation, as was illustrated by Ildoo Hwang (Pohang University of Science and Technology, South Korea). He reported that GLYCOGEN SYNTHASE KINASE3 (GSK3s) of the BRASSINOSTEROID INSENSITIVE2 (BIN2)/BIN2-LIKE (BIL) family can directly activate ARF7 and ARF19 by phosphorylation under the regulation of the CLAVATA3/endosperm surrounding region-related (CLE) peptide family (Cho et al., 2014). In addition, Sara Simonini from Lars Ostergaard's laboratory (John Innes Centre, Norwich, UK) presented evidence that auxin can also regulate the activity of ARFs, exemplified by ETTIN/ARF3, through direct binding, modulating its interaction with several transcription factors (Simonini et al., 2016). Some ARFs can thus also act as auxin receptors, illustrating a previously unsuspected collection of mechanisms acting at different levels in the auxin signaling pathway to regulate auxin-induced gene transcription.

Specificity of ARF-dependent regulation

Recent years have seen major advances in understanding how ARFs and Aux/IAAs regulate transcription. The structure of the PB1 domain, which allows for ARF and Aux/IAAs multimerization, was resolved (Parcy et al., 2016), as was that of the ARF1 and ARF5 DNA-binding domain, as discussed by Roeland Boer (Synchrotron ALBA, Cerdanyol del Valles, Spain). This work shows that ARFs dimerize through their DNA-binding domain and suggests that the distance between target sites in promoters determines the specificity of ARF binding on everted site repeats (Boer et al., 2014). A new preferred motif, TGTCGG, was also found in this study, a result supported by a bioinformatic analysis of promoters of auxin-induced genes (Zemlyanskaya et al., 2016) presented by Victoria Mironova (Novosibirsk State University, Novosibirsk, Russia). Moreover, Andrea Gallavotti (Waksman Institute, Rutgers University, Piscataway, NJ, USA) discussed a DNA affinity purification sequencing (DAP-seq) approach that has identified binding sites on naked genomic DNA for several ARFs from both *Arabidopsis* and maize (O'Malley et al., 2016). He showed that ARFs have some spacing specificities not only on everted repeats but also on inverted and direct repeats. His laboratory has now used DAP-seq with all maize-activating ARFs and a subset of repressing ARFs, and their findings suggest that repressing ARFs might bind to a similar but slightly longer motif. This, together with spacing specificities, would explain the observation that both specific and shared binding sites are found for both types of ARFs. Mingtang Xie from Joe Ecker's laboratory (The Salk Institute for Biological Studies, La Jolla, CA, USA) completed the picture by providing the first demonstration that Aux/IAAs and ARFs colocalize on DNA *in vivo*, using chromatin immunoprecipitation (ChIP)-Seq for a large number of ARFs and Aux/IAAs. The data he presented also suggested a high degree of flexibility in the spacing between sites. Thus, while spacing specificity is observed, it might not be the only parameter explaining the binding of ARFs to specific promoters. The fact that the same promoters are targeted by both activating and repressing ARFs appears to be an ancestral property that is already observed in the moss *Physcomitrella patens*, based on evidence presented by Mark Estelle (Lavy et al., 2016).

Non-transcriptional responses to auxin

Despite several lines of evidence establishing the non-essentiality of ABP1 function (Dai et al., 2015; Gao et al., 2015; Michalko et al., 2015, 2016), as discussed by Klaus Palme, auxin non-transcriptional responses were still attracting attention during the meeting. For example, Tongda Xu (Shanghai Center for Plant Stress Biology, Shanghai, China) reported that the ABP1-interacting receptor-like kinase TRANSMEMBRANE KINASE (TMK) (Xu et al., 2014) might mediate auxin signaling from the plasma membrane to the nucleus. At the plasma membrane, the C-terminal end of TMK is cleaved upon auxin treatment and this cleavage is favored by the presence of ABP1. The cleaved C-terminal of TMK then relocates to the nucleus where it interacts with a set of Aux/IAA proteins, thus modulating auxin signaling. It has also been reported that calcium (Ca^{2+}) signaling regulates auxin activity during development (Shih et al., 2015), with modifications in cytosolic Ca^{2+} levels being induced by auxin in a TIR/AFB-independent manner. Steffen Vanneste (Plant Systems Biology, VIB, Ghent University, Belgium) is currently investigating this process using a chemical biology approach. Using inhibitors identified in a chemical screen for inhibitors of auxin-induced Ca^{2+}, he and his team revealed that cytosolic Ca^{2+} signaling in plants participates in regulating PIN trafficking at least at the level of endocytosis. Also using a chemical biology approach, Ken-Ichiro Hayashi (Okayama University of Science, Okayama, Japan) described a novel chemical probe that can modulate PIN localization and auxin transport, independently of the TIR/AFB signaling pathway. Identification of the target of this probe could provide new insights into non-transcriptional responses to auxin.

Auxin and development

Auxin is central to most plant developmental processes, as illustrated by almost all the presentations during the meeting, many of which used the DII-VENUS auxin biosensor and its ratiometric derivative R2D2 (Brunoud et al., 2012; Liao et al., 2015) to assess auxin distribution. For example, several talks showed how coordinated auxin biosynthesis and transport drive reproductive organ and seed development. Both processes are indeed required for gynoecium patterning, as shown by Eva Sundberg (Swedish University of Agricultural Sciences, Uppsala, Sweden). Rita Batista from Claudia Köhler's laboratory (Swedish University of Agricultural Sciences, Uppsala, Sweden) presented evidence that fertilization triggers auxin biosynthesis in the egg cell and that transport of auxin to the seed coat allows for its development by removing a block imposed by epigenetic regulation through Polycomb Group (PcG) proteins (Figueiredo et al., 2016). Hélène Robert (CEITEC Masaryk University, Brno, Czech Republic) presented further evidence that auxin produced in seed maternal tissues is required during the earliest step of embryo development, in addition to auxin produced in the embryo itself (Robert et al., 2013). This identifies an interesting mechanism of coordination between maternal and embryonic tissues during seed development. Spatial control of auxin biosynthesis is also important for post-embryonic development. Indeed, Shuang Wu (Fujian Agriculture and Forestry University, Fuzhou, China) showed that blocking plasmodesmata in the root quiescent center induces differentiation of the surrounding stem cells [as previously observed using laser ablation experiments (van den Berg et al., 1997)] and coincidentally disrupts auxin accumulation at the root tip by inhibiting local auxin biosynthesis. This suggests that symplastic connections are involved in coordinating not only the transport (Wu et al., 2016) but also the biosynthesis of auxin.

Concerning root development, Ben Scheres (Wageningen University, Wageningen, The Netherlands) discussed how

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PLETHORA (PLT) transcription factors function downstream of auxin. *PLT* transcription is slowly induced by auxin, a dynamic that is essential for establishing a PLT gradient and for root tip functional zonation (Mähönen et al., 2014). Scheres provided strong genetic evidence that PLTs act early during lateral root development, mediating a symmetry break necessary for the generation of a new growth axis. Several talks explored the role of auxin in lateral root initiation and development. Although lateral root development requires the reprogramming and division of pericycle cells, Joop Vermeer (Zürich University, Zürich, Switzerland) showed that the early development of lateral roots requires auxin-mediated spatial accommodation of the overlaying tissues (Vermeer et al., 2014). Transcriptomic analyses of this developmental process suggest a combinatorial involvement of cell wall remodeling, changes in cytoskeleton activity, endomembrane trafficking and ion channel activity. Alexis Maizel (University of Heidelberg, Germany), who used light-sheet microscopy to extract rules for cellular behaviors during lateral root initiation and early development, showed tight control of lateral root founder cell asymmetric division preceding the formation of a layered organization (von Wangenheim et al., 2016). He further discussed that auxin might coordinate lateral root development and changes in the overlying tissues by controlling cortical microtubule dynamics. This would provide a way for auxin to influence cell geometries and cell division planes, in line with published observations in the embryo (Yoshida et al., 2014). A role for cell wall remodeling downstream of auxin in the developing lateral root is also known (Swarup et al., 2008), and Priya Ramakrishna (Ives de Smet's laboratory, University of Nottingham, Nottingham, UK) showed that the expansin EXPA1 could be an important player in the early stages of this developmental response.

Siobhan Braybrook (Sainsbury Laboratory, University of Cambridge, Cambridge, UK) further discussed how auxin regulates growth of tissues through modifications of their mechanical properties, this time in hypocotyls. She presented atomic force microscopy data showing that changes in pectin chemistry are likely instrumental to induce growth changes, as occurs in other developmental contexts (Peaucelle et al., 2011). Although auxin is known to be involved in pectin chemistry (Braybrook and Peaucelle, 2013), its role is still unclear, but Braybrook suggested that auxin could control the directionality of growth rather than its intensity. This is reminiscent of what has been observed during flower initiation at the shoot apical meristem (Sassi et al., 2014). Concerning the shoot apical meristem, Yuling Jiao (Institute of Genetics and Developmental Biology, Beijing, China) showed that polar auxin transport provides positional cues for setting the adaxial-abaxial polarity of leaves (Qi et al., 2014). In addition, he showed that auxin acts on meristem size by stimulating stem cell differentiation. It has also been suggested that feedback between auxin transport activity and cell polarity could explain the properties of the PIN1 network in the meristem and, while this mechanism is still elusive, Neha Bhatia now showed that MP/ARF5 acts in this feedback (Bhatia et al., 2016). She demonstrated that MP expression directly follows auxin distribution and that MP activity regulates PIN1 distribution. Finally, Marta Laskowski (Oberlin College, Oberlin, IH, USA) discussed that phase changes might set shoot and root architecture by affecting phyllotaxis transition and lateral root positioning in seedlings, a phenomenon that is dependent on auxin transport and distribution. Overall, these various presentations illustrated that auxin acts at multiple scales to shape the dynamics of plant growth and development.

The role of auxin in response to environmental stimuli

Auxin-mediated modulation of plant development in response to environmental conditions was a frequent theme throughout the meeting. Eilon Shani, for example, showed that DEHYDRATATION-RESPONSIVE-ELEMENT-BINDING (DREB) protein/C-REPEAT BINDING FACTORS (CBFs) promote the expression of a set of Aux/IAAs in response to abiotic stress, and that plant stress tolerance requires auxin-sensitive Aux/IAA transcriptional repressors. Yan Xiong (Shanghai Institution of Biological Sciences, Shanghai, China) described his work on auxin accumulation in response to light, involving TARGET OF RAPAMYCIN (TOR) kinase, a central regulator of metabolic sugar signals in the root apical meristem (Xiong et al., 2013). His latest work shows that TOR integrates not only sugar signals but also light signaling in the shoot apex through light-dependent auxin accumulation. These results are reminiscent of a recent report showing that TOR kinase integrates light and metabolic signals for stem cell activation at the shoot apex (Pfeiffer et al., 2016). Chloé Béziat (Jürgen Kleine-Vehn's laboratory, BOKU, Vienna, Austria) discussed how the expression of PIN-LIKES (PILS) auxin transporters is stimulated by light, consequently modulating auxin signaling that is essential for phototropic opening of the apical hook, which otherwise protects the meristem of seedlings as they grow in the dark. Christian Frankhauser (University of Lausanne, Lausanne, Switzerland) discussed the role of PHYTOCHROME B (PHY B) in modulating phototropism by regulating transcription factors of the PHYTOCHROME INTERACTING FACTOR (PIF) family in photoautotrophic seedlings. He demonstrated that shade-promoted phototropism is a gradual reaction linked to *YUC* activation by PIFs in cotyledons (Goyal et al., 2016). Furthermore, Jorge Cassal (University of Buenos Aires and CONICET, Buenos Aires, Argentina) showed that a low PHYB concentration induces CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) E3 ligase abundance, mediating degradation of negative regulators of PIF and therefore providing evidence that a COP1-dependent loop is necessary for the early response to shade (Pacín et al., 2016).

Auxin involvement in cold responses was elegantly presented with reference to *Arabis alpina*, a perennial plant that has to maintain its growth by vegetative branches or dormant buds (Wang et al., 2009). Alice Vayssière (Maria Albani's laboratory, University of Cologne, Cologne, Germany) showed that the adaptation to an alpine environment by this species is controlled by *PERPETUAL FLOWERNG 1* (*PEP1*). *PEP1* expression is downregulated during vernalization such that flowering is initiated in some meristems, but upregulated after vernalization to repress flowering in the remaining meristems, which remain vegetative (Wang et al., 2009). The outgrowth of the inflorescence and vegetative branches is only stimulated when temperatures get warmer and result in transient increases in IAA levels in different stem parts. Jiří Friml (IST Austria, Klosterneuburg, Austria) described how auxin functions in the response to gravity in *Arabidopsis* hypocotyls, during which time the polarization of auxin transport via the action of PIN3 is known to be essential for increased auxin response at the lower side of the hypocotyl, inducing bending. He completed this story by describing the existence of a loop in which auxin feeds back onto PIN3 localization at the later stages of the gravity response, where a symmetrical pattern of PIN3 is re-established to stop the hypocotyl bending (Rakusová et al., 2016). Stefan Kepinski (University of Leeds, Leeds, UK) also focused on the response to gravity, this time in the root, and in particular on the regulation of gravity set point angle (GSA: the angle at which an organ is maintained with respect to gravity). He showed that, similar to shoot branches (Roychoudhry et al., 2013), lateral roots are actively maintained

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at non-vertical GSA and must therefore integrate positive and negative gravitropic responses, the latter being driven by PIN-mediated auxin transport and the TIR/AFB signaling system. Auxin is also involved in the response to abiotic stress, and this was illustrated by Zhaojun Ding (Shandog University, Jinan, China) who showed that root growth inhibition in the presence of aluminum is due to increased auxin biosynthesis (Liu et al., 2016). Finally, plant interactions with pathogens are also controlled by auxin to some extent; an example of this was discussed by Barbara Kunkel (Washington University, St Louis, Mo, USA), who showed that *Pseudomonas syringae* manipulates phytohomorne signaling to promote pathogenesis. She demonstrated that auxin synthesized by the bacterium, which it produces through a novel pathway, promotes pathogen growth by suppressing the salicylic acid (SA)-mediated defense response of its host. Furthermore, Ulrike Mathesius (Australian National University, Canberra, Australia) discussed what makes root bacteria-induced nodules distinct from lateral roots. One part of the answer relies not only on the regulation of the auxin transport machinery, but also on the auxin response, which is different in nodule and lateral root formation, with specific sets of Aux/IAAs having specific functions in these two developmental contexts.

Interactions of auxin with other signaling molecules

The plethora of developmental aspects controlled by auxin might be explained by its ability to crosstalk with other signaling molecules. Indeed, this crosstalk was a recurrent topic during the entire meeting.

Cytokinins, for example, influence many aspects of auxin biology, starting with their action on auxin biosynthesis. Yi Tao (Xiamen University, Xiamen, China) described the binding of ARABIDOPSIS RESPONSE REGULATOR 1 (ARR1), which is involved in cytokinin signaling, to two specific cis-elements of TAA1, which is implicated in the shade-induced synthesis of indole-3-pyruvate (IPA) – a precursor of IAA. Lucia Strader showed that the number of tonoplast-localized TOB1 transporters, which transport IBA, increases upon cytokinin treatment, thus demonstrating crosstalk between cytokinins and IBA sequestration during lateral root development. Moreover, during gynoecium development, cytokinins influence auxin homeostasis by positively regulating *PIN7* expression in order to drain auxin from the medial domain, as reported by Eva Sundberg. Ulrike Mathesius also described how cytokinins have different effects during nodule and lateral root development. In *Medicago trucatula*, auxin maxima that are formed at sites of initiating nodules are controlled via inhibition of acropetal auxin transport by flavonoids, the synthesis of which is positively regulated by cytokinins. By contrast, cytokinins have inhibitory effects on lateral root initiation, and the control of auxin transport by cytokinins does not require flavonoids.

Crosstalk between auxin and other plant hormones was also discussed. Marcel Quint (Martin Luther University of Halle-Wittenberg, Halle, Germany) demonstrated a downstream effect of brassinosteroids on auxin regulation for thermomophorgenesis. Crosstalk between these two phytohormones was also extensively discussed by Zhi-Yong Wang (Carnegie Institution for Science, Stanford, CA, USA). He notably showed that brassinosteroids and auxin display similar effects in shoots but opposite effects in roots on genes involved in cell elongation, suggesting a crucial balance between these two phytohormones in order to promote root growth (Chaiwanon and Wang, 2015). Crosstalk between auxin and jasmonic acid was presented by Catherine Bellini (Umeå University, Umeå, Sweden/IJPB, Versailles, France) who showed that, during adventitious root development, a specific set of ARFs control *GH3* expression, which in turn modulates jasmonic acid activity (Gutierrez et al., 2012). Furthermore, Catherine Bellini suggested a possible regulation of jasmonic acid biosynthesis by auxin. Using a transcriptomic approach (Lewis et al., 2013), Gloria Muday (Wake Forest University, Winston Salem, NC, USA) identified transcripts linked to the antagonist effects on ethylene and auxin on lateral root formation, and their synergetic action on root elongation and root hair formation. Ottoline Leyser (Sainsbury Laboratory, University of Cambridge, Cambridge, UK) discussed crosstalk between strigolactones and auxin in the regulation of shoot branching, involving modulation of auxin transport and of expression of the transcription factor *BRANCHED1* (*BRC1*). She reported that strigolactones modulate axillary bud activity by inhibiting the feedback of auxin on its own transport by removing PINs from the plasma membrane and by regulating *BRC1* expression. Finally, Toshiaki Tameshige (Nagoya University, Nagoya, Japan) described how crosstalk between the cysteine-rich peptide, EPIDERMAL PATTERNING FACTOR LIKE (EPFL) and auxin is involved in a feedback loop that regulates leaf serration.

Auxin through plant evolution

Given its diverse roles, auxin is thought to have been crucial during plant evolution. While most presentations discussed thus far used *Arabidopsis* as a model species, several explored how auxin functions in different angiosperms and basal plant species, and how auxin-related functions could have evolved and contributed to plant evolution. For angiosperms, the genetic analysis of how auxin transport, biosynthesis and signaling contribute to maize development is progressing fast. Paula McSteen (University of Missouri, Columbia, MO, USA) discussed how studies of various maize mutants are consolidating our knowledge on the essential role of auxin in producing shoot lateral structures, as most mutants are affected in tassel and ear development. She also presented the characterization of BARREN STALK2 (BA2), which might act in a dimer with BA1 downstream of auxin. This mechanism is conserved in rice, and McSteen presented a transcriptomics approach that could help to identify both conserved and divergent regulators of auxin-dependent lateral structure development in angiosperms. The moss *Physcomitrella patens* and the liverwort *Marchantia polymorpha* possess reduced numbers of ARFs and Aux/IAAs, providing simplified configurations to understand auxin signaling and its evolution, as highlighted by Mark Estelle. Indeed, Eva Sundberg showed that genes encoding homologs of *Arabidopsis* auxin biosynthesis enzymes and auxin influx and efflux carriers are expressed in the egg cell, in the antheridia, and during sperm development in *Physcomitrella*. This strengthens the idea that a broad role for auxin in reproductive development already existed in moss (Landberg et al., 2013). In addition, Mitsuyasu Hasebe (National Institute for Basic Biology, Okazaki, Japan) used live-imaging and various reporters for regulators of auxin transport and levels (biosynthesis, conjugation) to demonstrate a key role for changes in auxin concentration in cell identity switches and in dynamically driving *Physcomitrella* development. Takayuki Kohchi (Kyoto University, Kyoto, Japan) discussed the fact that auxin is required throughout the life cycle of *Marchantia*, which has the simplest set of auxin signaling components identified so far, as illustrated by the phenotypes observed in inducible lines expressing an auxin-insensitive MpAux/IAA (Kato et al., 2015). As in *Physcomitrella* (Lavy et al., 2016), these phenotypes suggest a role for auxin in growth, cell division, meristem activity and reproduction that has been conserved up to the angiosperms.

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Hirotoka Kato from Dolf Weijers' laboratory (University of Wageningen, Wageningen, The Netherlands) analyzed functional divergence between the three ARFs of *Marchantia*. His analysis suggests that MpARF1 is an activating ARF, whereas the two others are repressing ARFs (Kato et al., 2015), with all three exhibiting a general organization in functional domains very similar to *Arabidopsis* ARFs. Hirotaka Kato also showed that ARFs were already present in charophytes, while Aux/IAA and TIR1/AFB could not be detected. The origin of ARFs thus precedes the appearance of land plants, and ARFs could have originally functioned independently of auxin. Virginia Armbrust (University of Washington, Seattle, WA, USA) further showed that auxin has also been found as a signal that stimulates cell division of some marine diatoms and is emitted by bacteria associated with the diatoms (Amin et al., 2015). Moreover, homologs of auxin influx carriers have been found that could mediate the intake of auxin by the diatom. Active auxin transport could thus be of a very ancient origin, as could the role of auxin in the control of cell division.

Modeling and synthetic biology approaches to understanding auxin function

Among the many approaches used to understand auxin function, the increasing use of modeling tools was striking at this meeting. The presentation of Ottoline Leyser on the control of shoot branching by hormones illustrated how auxin transport canalization models have led to the idea that an auxin transport switch could integrate competition between different auxin sources and explain how auxin acts in the control of bud activation (Prusinkiewicz et al., 2009). Yuling Jiao similarly used an auxin canalization model suggesting that competition between emerging leaves and the center of the meristem is essential for controlling the size of the stem cell niche at the shoot apical meristem. The timing of lateral organ initiation at the shoot apical meristem is established by auxin-based inhibitory fields, and Teva Vernoux (École normale supérieure de Lyon, Lyon, France) showed that this timing is noisy, inducing defects in shoot phyllotaxis (Besnard et al., 2014). He further demonstrated that including stochasticity in signal perception in an inhibitory-field model can recapitulate these biological observations, suggesting that making a new organ in response to auxin and other signals could be based on a probabilistic decision (Refahi et al., 2016). Riccardo di Mambro from Sabrina Sabatini's laboratory (La Sapienza University, Rome, Italy) showed how they used a cell-based auxin transport model to analyze the interaction between auxin and cytokinins in setting root meristem size. Their analysis suggests that cytokinins, via the regulation of auxin degradation and polar transport, determine the localization of an auxin minimum at the upper boundary of the meristem that is required to set meristem size. Several presentations also illustrated how modeling can be used to understand the role of abiotic and biotic factors in modulating auxin-dependent development. Kirsten ten Tusscher (Utrecht University, Utrecht, The Netherlands) showed that a cell-based model allowed them to understand the regulation of halotropism (when roots grow away from salt) by auxin. Although a major role for PIN2 had been established, the model further pointed to important roles for positive feedback by auxin on both auxin efflux and influx (van den Berg et al., 2016). In his analysis, discussed above, Alexis Maizel also used cell-based models to establish that layer formation in lateral roots is an emergent property resulting from both the deformation pattern of the tissue and from the orientation of cell division (von Wangenheim et al., 2016). Eva Deinum (Wagenigen University, Wageningen, The Netherlands) also used modeling in the context of symbiosis to suggest that a diffusible signal coming from the epidermis could trigger the local accumulation of auxin, allowing for nodule initiation through interaction with auxin transport (Deinum et al., 2016). Ben Scheres further highlighted the power of modeling to understand auxin-dependent processes at a cellular scale. He explained how modeling microtubule biochemistry in realistic cell shapes obtained from early embryo segmentation has allowed him and his colleagues to predict and test when and where auxin could bias microtubule organization, a mechanism that could be essential for the activity of auxin in orienting cell division.

Synthetic biology has also emerged in recent years as a powerful approach to understand biological mechanisms. It has been applied to auxin by reconstructing the auxin signaling pathway regulating transcription in yeast (Pierre-Jerome et al., 2014), as discussed by Amy Lanctot from Jennifer Nemhauser's laboratory (Washington University, Seattle, WA, USA). She further showed how this synthetic pathway can be used to analyze how the organization of ARF-binding motifs in promoters influences binding and transcriptional activity, an analysis that supports the idea that it is not only binding site spacing that determines activity in response to a given ARF but also the number and orientation of sites (Pierre-Jerome et al., 2016). Eric Klavins (Washington University, Seattle, WA, USA) further discussed how the logic underlying the auxin pathway can be used to design synthetic networks and even cell-cell communication systems (Khakhar et al., 2016). He also showed that an inducible auxin-degradable transcription factor can allow the design of a switch that controls growth in yeast. His presentation provided an original perspective on how the knowledge that has accumulated over the years on auxin can be used to design new biological functions in organisms other than plants.

Conclusions

The Auxin 2016 meeting illustrated our ever-increasing knowledge on the transcriptional regulation of auxin, how it works cooperatively with other signals in many developmental processes and stress responses, as well as the long evolutionary history of this key plant hormone. Of note, the increasing use of modeling approaches is contributing to a better understanding of how auxin acts at multiple scales, allowing one to foresee how such approaches will be valuable in the coming years for illuminating the mechanisms underlying the versatile functions of auxin in plant development. The progress to come will undoubtedly make the next Auxin meeting as exciting as this one.

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Competing interests

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